Interspecific competition in a pecan–cotton alleycropping system in the southern United States: Production physiology

Diomides S. Zamora, Shibu Jose, P.K.R. Nair, and Craig L. Ramsey

Abstract: A study was conducted on a Red Bay sandy loam soil (Rhodic Paleudult) in Jay, Florida, USA, to investigate how interspecific interactions between pecan (*Carya illinoensis* K. Koch) and cotton (*Gossypium hirsutum* L.) would affect cotton leaf morphology and gas exchange and thereby biomass and lint yield. We quantified specific leaf area (SLA), specific leaf nitrogen (SLN), net photosynthesis (*A*), transpiration, stomatal conductance, and net canopy photosynthetic index (CNPI) from cotton with and without aboveground and belowground interactions. To separate roots of cotton and pecan, polyethylene-lined trenches were installed (barrier treatment) parallel to tree rows in half the number of plots. Results showed that SLA for barrier and nonbarrier plants was 61% and 47% higher, respectively, compared with the monoculture cotton. Monoculture plants exhibited higher CNPI ($70.7\ \mu mol \cdot m^{-2} \cdot s^{-1}$) compared with the barrier ($52.7\ \mu mol \cdot m^{-2} \cdot s^{-1}$) and nonbarrier plants ($18.3\ \mu mol \cdot m^{-2} \cdot s^{-1}$). SLN was similar for both the barrier and nonbarrier plants; however, it was lower than the monoculture. A positive curvilinear relationship between *A* and SLN was observed, with peak *A* ($28\ \mu mol \cdot m^{-2} \cdot s^{-1}$) observed between 2.2 and 2.4 mg $N \cdot m^{-2}$. Significant curvilinear relationships between CNPI and aboveground biomass and lint yield were also observed for all treatments. These findings indicate that competitive interactions in alleycropping regulate leaf level traits such as SLA and SLN by altering water and light availability, which in turn exert a profound influence on aboveground biomass and lint yield for cotton plants.

Key words: aboveground and belowground competition, net canopy photosynthetic index (CNPI), net photosynthesis, photosynthetically active radiation (PAR), specific leaf area, specific leaf nitrogen.

Résumé : Les auteurs ont conduit une étude dans un loam sableux (paleudulte rhodique) à Red Bay, dans la région de Jay, en Floride, aux USA, afin d'examiner comment les interactions interspécifiques entre le pacanier (*Carya illinoensis* K. Koch) et le coton (*Gossypium hirsutum* L.) affectent la morphologie foliaire du coton et ses échanges gazeux, et conséquemment sa biomasse et son rendement en fibre. Ils ont quantifié la surface foliaire spécifique (SLA), l'azote foliaire spécifique (SLN), la photosynthèse nette (*A*), la transpiration, la conductance stomatale ainsi que l'index photosynthétique de la canopée (CNPI), chez le coton avec ou sans interactions au-dessus ou au-dessous du sol. Afin de séparer les racines du coton et du pacanier, on a installé des tranchées délimitées par du polyéthylène (traitement isolement), parallèlement aux rangées d'arbres, dans la moitié des parcelles. Les résultats montrent que la SLA chez les plantes isolées et non isolées est de 61 % et 47 % plus élevée, respectivement, comparativement au coton en monoculture. Les plants en monoculture montrent un CNPI plus élevé ($70.7\ \mu mol\ m^{-2} \cdot s^{-1}$) comparativement aux traitements isolés ($52.7\ \mu mol\ m^{-2} \cdot s^{-1}$) et non isolés ($18.3\ \mu mol \cdot m^{-2} \cdot s^{-1}$). Le SLN est semblable chez les plantes isolées ou non; cependant, il est plus faible qu'en monoculture. On observe une corrélation curvilinéaire positive entre *A* et SLN, avec un pic en *A* ($28\ \mu mol\ m^{-2} \cdot s^{-1}$) observé avec 2.2 à 2.4 mg $N \cdot m^{-2}$. On observe également des relations curvilinéaires significatives entre le CPNI et la biomasse et fibre au-dessus du sol, chez tous les traitements. Ces constatations indiquent que des interactions compétitives, dans la culture en allées, règlent des caractères foliaires comme la SLA et la SLN, en altérant les disponibilités en eau et en lumière, lesquelles à leur tour exercent une profonde influence sur les rendements en biomasse et en fibre.

Mots clés : compétition épigée et hypogée, index photosynthétique net de la canopée (CNPI), photosynthèse nette, radiation photosynthétique active (PAR), surface foliaire spécifique, azote foliaire spécifique.

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Introduction

It is well known that canopy level mechanisms influence growth and yield in plants. Leaf-level traits such as specific leaf area (SLA), specific leaf nitrogen (SLN), and net photosynthesis (P_{net}) have all been explored in explaining growth and yield in agronomic and forestry systems (Reich et al. 1998*a*, 1998*b*, 1999; Zhao and Oosterhuis 1998; Gillespie et al. 2000; Gazal and Kubiske 2004). These traits, which influence carbon fixation and allocation patterns in plants (Evans 1989; Sinclair et al. 1993; Muchow and Sinclair 1994; Pettigrew et al. 2000; Milroy and Bange 2003), are

greatly influenced by resource (light, water, and nutrients) competition and availability.

Plants develop and grow differently under different environmental conditions. All plants respond morphologically and physiologically to shade and vary considerably in regard to their shade tolerance. Plants that grow in a low-light environment, such as those plants grown in alleycropping agroforestry systems, invest relatively more of the products of photosynthesis and other resources in building greater leaf surface area, resulting in thinner leaves and higher specific leaf area (SLA). This, in turn, is associated with relatively fewer and smaller palisade and mesophyll cells, which may affect the photosynthetic capacity per unit leaf area. In contrast, plants grown in full sun develop thicker leaves, which contain more photosynthetic apparatus and thereby exhibit a higher rate of P_{net} per unit leaf area (Pettigrew et al. 1993; Lambers et al. 1998; Taiz and Zeiger 2000). Thus, low light intensity limits photosynthesis and thereby net carbon gain and plant growth. High light intensity may also limit photosynthesis, particularly if other factors are not optimal (Lambers et al. 1998).

Alleycropping is a major form of agroforestry in the USA, which involves cultivation of woody perennials, usually for nut production, in rows, while crops are cultivated between the rows of trees (Garrett and Buck 1997; United States Department of Agriculture (USDA) 1999). Alleycropping systems can be used to optimize land production. However, without proper management, trees and crops possess a high potential for interspecific competition for resources (e.g., light, water, and nutrients) that may limit production.

Light is a major competitive vector in alleycropping systems. The photosynthetic response of understory plants to shading may also depend on the carbon fixation pathways of the associated crop species. It is well known that the photosynthetic rate of C_3 plants increases sharply as photosynthetically active radiation (PAR) increases from deep shade up to approximately 25%–50% of full sunlight, then peaks and remains constant with increasing light. However, C_4 species do not become light saturated, and the photosynthetic rate continues to increase up to full sunlight (Monteith 1978; Kozlowski and Pallardy 1997; Lambers et al. 1998). As a result, C_3 crop plants may be better suited for alleycropping than C_4 plants. For example, a study by Gillespie et al. (2000) in the midwestern United States showed substantial reduction in photosynthetic rates of maize (*Zea mays* L.), a C_4 species, in a black walnut (*Juglans nigra* L.) alleycropping system. A 45% reduction in PAR resulted in 40% decrease in P_{net}. However, cotton, a C_3 species, was light saturated at 50% of the full sun and hence was not affected as much by shading in another study (Milroy and Bange 2003).

The importance of foliar N in photosynthesis is indicated by the well-known positive correlation between foliar N (either %N or SLN) and photosynthetic activity (Gulmon and Chu 1981; Field and Mooney 1986; Evans 1989; Harrington et al. 1989; Egli and Schmid 1999). Generally, sun leaves tend to have higher SLN than shade leaves (Hollinger 1996; Bond et al. 1999). SLA and SLN are also often negatively correlated across the canopy light gradient (Ellsworth and Reich 1993; Bond et al. 1999; Grassi and Minotta 2000; Stenberg et al. 2001). This N gradient results in efficient

use of canopy N in carbon fixation (Field 1983; Werger and Hirose 1991; Chen et al. 1993). Other feedback mechanisms (i.e., allocation of carbon to roots) also function to increase belowground biomass to enhance resource capture when nutrients such as N are limiting for photosynthetic processes. For instance, cotton planted as a monoculture in Arkansas with limiting N increased its root/shoot ratio to enhance resource capture for growth (Keino 1998).

Competition for water between system components can also affect agronomic productivity in alleycropping (Jose et al. 2000; Miller and Pallardy 2001; Wanvestraut et al. 2004). It is well known that intake of CO_2 decreases as water availability decreases, because of decreased stomatal conductance (Lambers et al. 1998; Taiz and Zeiger 2000). Decreased water availability can thus restrict P_{net} on a leaf area and mass basis, which often translates into reduced aboveground biomass productivity (Pereira et al. 1992; Davis et al. 1999; Samuelson 2000; Gazal and Kubiske 2004).

The physiological mechanisms affecting production in agroforestry systems have received limited attention both in the tropical and temperate regions of the world. This study was designed to examine how SLA and SLN would respond to aboveground and belowground competition for resources and how these mechanisms affect foliar and canopy level photosynthesis and thereby aboveground production. We hypothesized that SLA would be higher under shade in the alleycropping system compared with the monoculture. We also hypothesized that this would result in lower SLN for plants in alleycropping. A further reduction in SLN in the nonbarrier treatment compared with the barrier treatment was expected if competition for N existed. Changes in SLA and SLN would influence the overall canopy net photosynthesis, which, in turn, would affect biomass and lint yield.

Materials and methods

The study site

The study was conducted at the West Florida Research and Education Center farm of the University of Florida located in Jay, Florida, USA (30°47′N, 87°13′W). The climate is considered to be temperate with moderate winters and hot humid summers. The soil is classified as Red Bay sandy loam (fine-loamy, siliceous, thermic Rhodic Paleudult) with an average water table depth of 1.8 m. Average rainfall and air temperature during the 2002 growing season (June–October) was 585 mm and 24.31 °C, respectively (Fig. 1).

For the current study, a pecan (*Carya illinoensis* K. Koch) – cotton (*Gossypium hirsutum* L.) alleycropping system was established in 2001 from an existing orchard of pecan trees planted in 1954. The orchard was managed under nonintensive clover (*Trifolium* spp.) and rye grass (*Lolium* spp.) production for 29 years prior to the initiation of the current study (Allen et al. 2005). Twelve plots were demarcated within the orchard and arranged into six blocks using a randomized block design. Each plot, which consisted of two rows of trees oriented in a north–south direction, was 27.4 m long and 18.3 m wide, with a practical cultivable width of 16.2 m and was separated from each adjacent plot by a buffer zone of the same dimensions.

To assess tree root competition, each block was randomly divided into a barrier and nonbarrier plot. Barrier plots were

Fig. 1. Daily precipitation and temperature between 1 May and 31 October 2002 at the West Florida Research and Education Center research farm, Jay, Florida, USA.
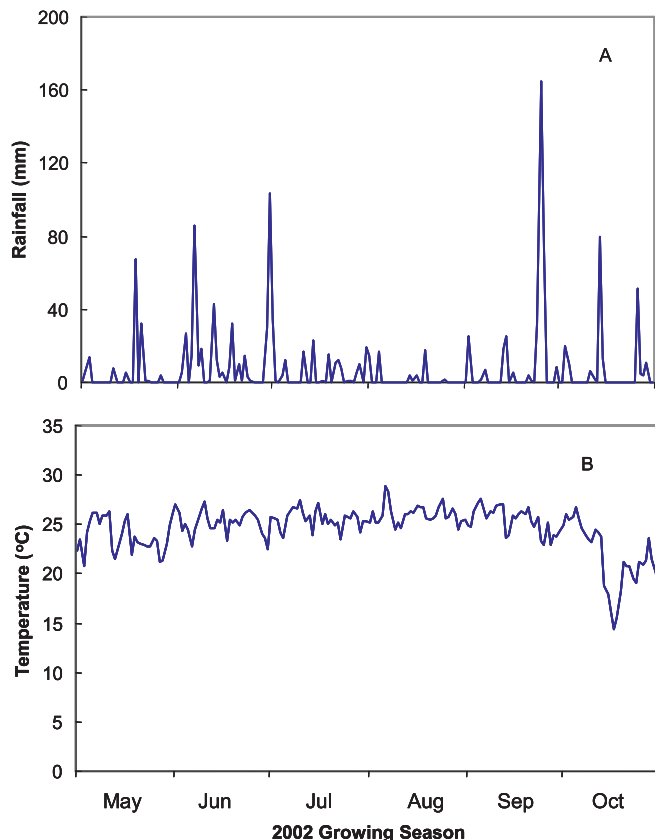
subjected to a root pruning treatment in March 2001, in which a trenching machine was used to dig a 0.2 m wide and 1.2 m deep trench along both sides of the plot at a distance of 1.5 m from the tree line to separate the root systems of pecan and cotton. Trenches were lined with 0.15 mm thick polyethylene sheets prior to mechanical backfilling. The barrier plots served as the tree-root exclusion treatment (referred to as barrier treatment) preventing interaction of tree and cotton roots, while the nonbarrier (referred to as nonbarrier treatment) served as the tree-root competition treatment. Sixteen rows of cotton, 1 m apart, were established in each plot. Cotton (DP458/RRvariety) seeds were planted in each row along a north–south orientation on 13 May 2002 using conventional tillage (15–20 cm deep) at a rate of 23 600 seeds/ha in the alley between the pecan tree rows.

For control purposes, three plots in an adjacent field were maintained as cotton monoculture (referred to as monoculture treatment). All treatments received standard inorganic fertilizer (3:9:18 (N–P–K) fertilizer at a rate of 89.6 kg N·ha^{-1}), and pesticide application for cotton in the southern US. No irrigation was applied.

Gas exchange measurements

Net photosynthetic rate (A) (μmol CO_2·m^{-2}·s^{-1}), transpiration rate (E) (mm H_2O·m^{-2}·s^{-1}), and stomatal conductance (g) (mm·m^{-2}·s^{-1}) were measured using a LICOR 6400 (LI-COR, Lincoln, Nebraska) portable infrared gas analyzer

(IRGA). Measurements were made four times on a monthly interval from June to September 2002, on the uppermost and fully expanded main-stem leaves of three cotton plants in the first, fourth, and eighth rows. All measurements were taken between 1000 and 1500 h central daylight savings time under ambient conditions on clear sunny days. Instantaneous water use efficiency (WUE) defined as the ratio of A and E was calculated for each sampled leaf.

To determine whether light was a limiting factor in our system, maximum light saturated photosynthetic rate (A_{max}) and intercellular CO_2 (A–C_i) were also measured under constant light (i.e., 2000 μmol·m^{-2}·s^{-1}) at the peak of cotton growth in August 2002 using LICOR 6400. Photosynthetic light response curves were also generated for each treatment at the same time under constant air temperature (30 °C), relative humidity (60%), and CO_2 (370 ppm). Ambient light was used to generate A–C_i curves by measuring A under different CO_2 concentrations. Canopy net photosynthetic index (CNPI), an index of the canopy photosynthesis, was calculated as the product of A or A_{max} and canopy leaf area index (LAI). Canopy LAI was calculated from canopy biomass and specific leaf area (described below) for each treatment.

During A_{max} measurement for a specific plant, three soil samples (approx. 200 g) were collected near the base of the plants to a depth of 10 cm to determine gravimetric water content. Soil samples were weighed, oven dried for 72 h at a constant (105 °C) temperature, and reweighed to determine the gravimetric soil water content.

Specific leaf area (SLA) and foliar N

Leaves subjected to gas exchange measurements (six leaves total in each row per plot) were collected immediately after measurement to determine SLA. To avoid desiccation, leaves were placed in polyethylene bags, stored in a cooler and transported to the lab where leaf area was measured using a LICOR 3000 leaf area meter. Leaves were then oven-dried at 70 °C for a minimum of 72 h, ground using a coffee grinder, and analyzed for total Kjeldahl nitrogen. Leaf nitrogen concentration was multiplied by specific leaf mass to determine SLN.

Aboveground biomass and lint yield

Cotton plant parts such as leaves, stems, bolls, and flowers within 1 m × 1 m subplots were carefully harvested in each main plot. Harvested cotton plants were placed in paper bags, dried for 72 h at 70 °C, and then weighed. Lint yield (devoid of seeds) of cotton in each row (rows 1, 4, and 8) in each plot and in the monoculture was quantified from two 0.61 m × 6.1 m sections in each row.

Data analysis

Analysis of variance (ANOVA) within the framework of a randomized split block design was used to test for statistical differences in measured parameters using the mixed procedure of the SAS statistical software package (SAS Institute Inc., Cary, North Carolina). The Shapiro–Wilk's test was used to test all data for normality of distribution. Logarithmic ($\log(x + 1)$) transformation was performed to improve normality when necessary. Differences between means were determined using the least square means procedure. Treatment effects were considered significant at $\alpha = 0.05$. Regres-

Table 1. Specific leaf area (SLA) of cotton grown under different growth conditions in an alleycropping system in Jay, Florida.

	Specific leaf area (SLA)		
	Treatment		
Row	Nonbarrier	Barrier	Monoculture
1	267.2a (8.4)	270.6b (8.1)	
4	277.8a (9.0)	303.4a (10.6)	
8	269.4a (10.4)	314.1a (13.6)	
Overall mean	271.5 B (5.8)	296.6 A (6.4)	184.6C (10.6)

Note: Standard errors of the mean are given in parentheses. Within-treatment values followed by the same lowercase letter are not significantly different at the 0.05 level of probability. Computed P values for nonbarrier and barrier were 0.597 and 0.0038, respectively. The upper case letter represents treatment comparison. Values followed by the same capital letter are not significantly different at the 0.05 level of significance ($P < 0.0001$).

sion analysis was used to define relationships between SLN and A, CNPI and aboveground biomass, and CNPI and lint yield

Results

Specific leaf area, specific leaf nitrogen, and net photosynthesis

There were variations in cotton leaf morphology (leaf area and mass) among treatments resulting in differences in SLA (Table 1). The cotton in the barrier treatment had a higher SLA than that of the nonbarrier treatment plants. Monoculture plants, which exhibited higher leaf mass (0.47 g) and lower SLA, contained significantly higher SLN (2.30 g·m^{-2}) compared with those plants in the barrier (1.92 g·m^{-2}) and nonbarrier (1.99 g·m^{-2}) treatments (Fig. 2). No spatial variations in SLA among rows were found in the nonbarrier treatment, but SLA in row 1 of the barrier treatment was lower than rows 4 and 8 ($P = 0.0038$).

Barrier and monoculture plants had similar light response curves with light saturation occurring at about 50% of the full sun, whereas light saturation was observed at about 30% of the full sun in the nonbarrier treatment (Fig. 3). Light saturated maximum photosynthetic rate also varied accordingly. While A_{max} was 23 and 25 μmol CO_2·m^{-2}·s^{-1} for the barrier and monoculture plants, respectively, it was only 18 μmol CO_2·m^{-2}·s^{-1} for the nonbarrier treatment. Similarly, for any given intercellualar CO_2 concentration, cotton in nonbarrier treatment exhibited lowest A_{max} compared with the barrier and monoculture plants (Fig. 4). Analysis of gravimetric soil water content during A_{max} measurement showed that the nonbarrier treatment had lower soil water content (14.8%) than the barrier treatment (18.8%). Soil water content was the lowest (10.4%) in the monoculture treatment.

A positive curvilinear relationship between A and SLN was observed, with peak photosynthesis ($A = 26–28$ μmol CO_2·m^{-2}·s^{-1}) observed between 2.2 and 2.4 mg N·m^{-2} (Fig. 5). Since SLN did not differ significantly between the barrier and nonbarrier plants, it is reasonable to assume that
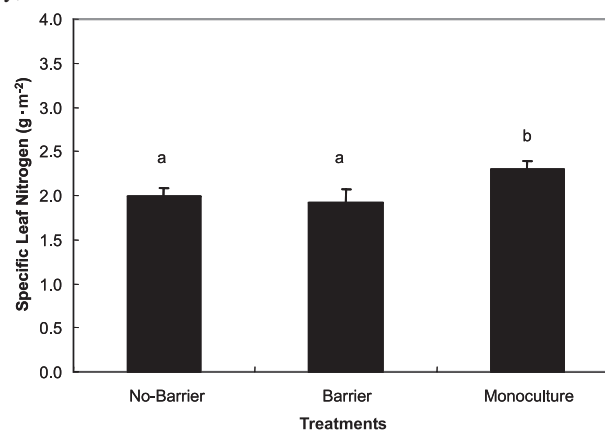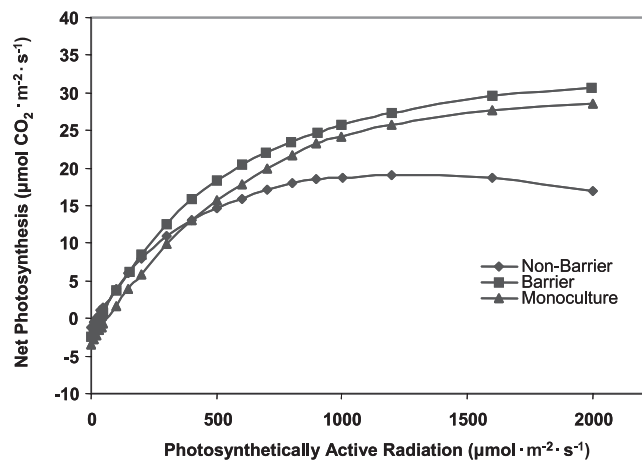
Fig. 2. Specific leaf nitrogen (SLN) content of cotton plants grown under different growth conditions in an alleycropping system in Jay, Florida.

Fig. 3. Light response curve of cotton in nonbarrier, barrier, and monoculture treatments in a pecan–cotton alleycropping system in Jay, Florida. Note: Measurement was made once during the mid-growing season (August).

Fig. 4. Intercellular CO_2 (A–C_i) curve of cotton in nonbarrier, barrier, and monoculture treatments in a pecan–cotton alleycropping system in Jay, Florida. Note: Measurement was made once during the mid-growing season (August).
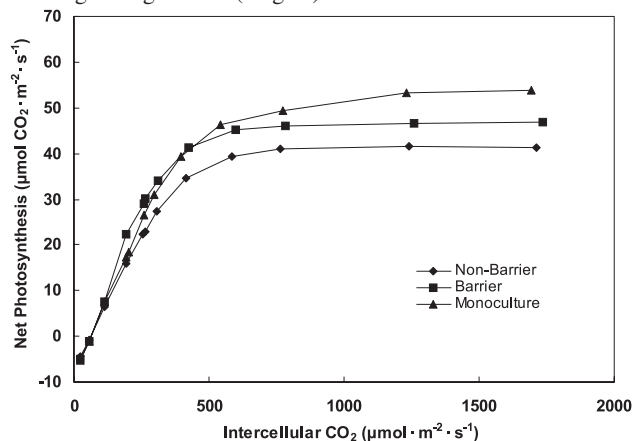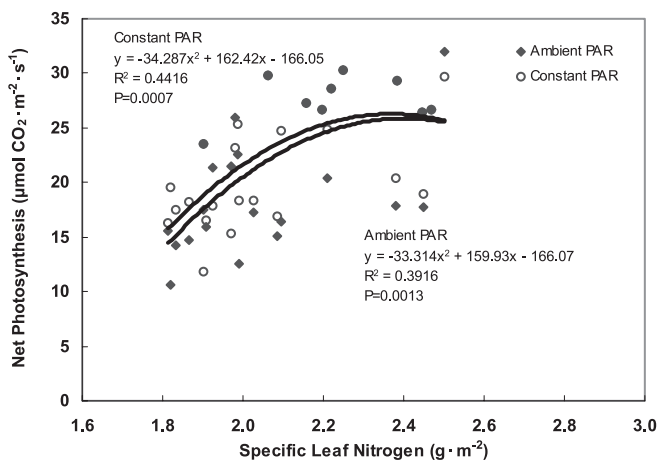

Fig. 5. Relationship between specific leaf nitrogen (SLN) and leaf level net photosynthesis of cotton in nonbarrier, barrier, and monoculture treatments in Jay, Florida.

the 56% reduction in A_{max} in the nonbarrier plants compared with barrier plants was not a result of decreased foliar N.

Both E and g were higher in the monoculture compared with the barrier and nonbarrier treatments (Table 2). The nonexclusion of cotton roots from pecan resulted in lower E and g in nonbarrier plants (51% and 68%, respectively), than those of the barrier plants. Water-use efficiency (WUE) (2.71 mmol·mol^{-1}) of the monoculture plants was not significantly different from nonbarrier plants (2.59 mmol·mol^{-1}). WUE in barrier plants (2.13 mmol·mol^{-1}), however, was much lower than those of the nonbarrier and monoculture plants.

Canopy net photosynthetic index versus biomass and lint yield

CNPI showed significant differences among treatments (Table 3). Monoculture treatment had the highest canopy A, which was 34% higher than the barrier treatment. Average canopy A in the barrier treatment was almost three times higher compared with the nonbarrier treatment ($P = 0.0429$).

The barrier treatment resulted in 65% increase in above-

ground biomass (exclusive of lint yield) of cotton plants compared with the nonbarrier (323.7 versus 195.9 g·m^{-2}, respectively) treatment. Aboveground biomass production in the monoculture plants was 307.01 g·m^{-2} and was statistically similar to the barrier but different from the nonbarrier ($P = 0.0303$) treatment. There were no inter-row variations in aboveground biomass among sampled rows. Alleviating belowground competition resulted in differences in cotton lint yield among treatments ($P = 0.0001$). Lint yield in the barrier treatment (51.02 g·m^{-2}) was three times higher than that of the nonbarrier treatment (17.06 g·m^{-2}). Lint yield was highest for the monoculture treatment (58.1 g·m^{-2}).

Mean aboveground biomass showed a strong and significant relationship with CNPI under ambient condition ($R^2 = 0.63$, $P < 0.0001$). The relationship was further improved ($R^2 = 0.77$) when A_{max} (measured under a constant PAR of 2000 μmol·m^{-2}·s^{-1}) was used in the analysis (Fig. 6). Similar relationships were also observed between CNPI and lint yield (Fig. 7). Maximum lint yield was obtained at an optimum CNPI of 65–70 μmol·m^{-2}·s^{-1}.

Discussion

Competition for resources in our system affected leaf morphology of cotton. The barrier plants outperformed the nonbarrier plants both in their leaf development and photosynthetic rates. Large differences were observed in SLA among these treatments that affected their gas exchange capacity. Cotton in the barrier and nonbarrier treatments had higher SLA than the monoculture (Table 1).

Foliage formed in low light often has lower A than foliage formed in high light and generally has different morphological and biochemical characteristics, such as higher SLA and lower leaf N (Cregg et al. 1993; Stenberg et al. 1994; Groninger et al. 1996; Jose et al. 2003; Nippert and Marshall 2003). Accordingly, many studies have demonstrated significant decline in A for plants growing under low light levels. We have observed this scenario in our experiment as well. Pecan trees caused an average 50% reduction of PAR transmittance to cotton in the alleys compared with cotton in monoculture treatment (800 μmol·m^{-2}·s^{-1} versus 1600 μmol·m^{-2}·s^{-1}) (Zamora et al. 2006b). Campbell et al. (1990) found that leaves of soybean (*Glycine max* L.) grown in full sun were capable of higher levels of photosynthesis, and became light saturated in full sun unlike leaves grown in lower light intensities. This reduction in photosynthesis was attributed to a decrease in leaf thickness (higher SLA) that led to lower chloroplast (Campbell et al. 1990; Paul and Foyer 2001) on a leaf area basis for plants grown under shade.

It is well established that foliar N and chlorophyll content are strongly correlated (Evans 1989). As a result, strong positive correlations between foliar N and A have been observed in a number of species (Evans 1989; Mitchell and Hinckley 1993; Bond et al. 1999; Egli and Schmid 1999). Many process models utilize foliar N as a scalar for integrating photosynthetic processes from leaf level to canopy level (Kull and Jarvis 1995; Leuning et al. 1995; Lai et al. 2002; Milroy and Bange 2003). The net photosynthetic rate of cotton in this study showed significant positive correlations with SLN ($R^2 = 0.44$ and $R^2 = 0.39$, for constant and ambi-

Table 2. Leaf level transpiration (E) and stomatal conductance (g) of cotton measured under ambient condition (photosynthetically active radiation (PAR) and CO_2 concentration) in a pecan–cotton alleycropping system in Jay, Florida.

| | Leaf level transpiration (E) ($mmol·m^{-2}·s^{-1}$) | | | | Leaf level stomatal conductance (g) ($mmol·m^{-2}·s^{-1}$) | | | |
| | Row 1 | Row 4 | Row 8 | | Row 1 | Row 4 | Row 8 | |
Treatment	Mean	Mean	Mean	Overall mean	Mean	Mean	Mean	Overall mean
Nonbarrier	4.73a (0.19)	5.03a (0.21)	5.09a (0.20)	4.95C (0.34)	0.31a (0.04)	0.33a (0.04)	0.30a (0.01)	0.31C (0.01)
Barrier	6.54b (0.31)	7.7a (0.30)	8.13a (0.34)	7.48B (1.13)	0.43b (0.03)	0.54ab (0.03)	0.57a (0.02)	0.52B (0.02)
Monoculture				12.65A (1.28)				1.12A (0.07)

Note: Standard errors of the mean are given in parentheses. The uppercase letters are for treatment comparisons. Means followed by the same capital letters are not significantly different at the 0.05 level of significance. The lowercase letters are within-treatment comparison among rows. Within-treatment values across the rows followed by the same lowercase letter are not significantly different at the 0.05 level of significance.

Table 3. Canopy net photosynthetic index (CNPI) of cotton measured under ambient condition (photosynthetically active radiation (PAR) and CO_2) in a pecan–cotton alleycropping system in Jay, Florida.

| | Canopy net photosynthetic index (CNPI) ($\mu mol\ CO_2·m^{-2}·s^{-1}$) | | | |
| | Row 1 | Row 4 | Row 8 | |
Treatment	Mean	Mean	Mean	Overall mean
Nonbarrier	17.43a (0.50)	18.10a (0.70)	19.44a (1.80)	18.32C (0.70)
Barrier	23.79b (1.80)	65.67a (2.20)	68.61a (2.30)	52.69B (2.10)
Monoculture				70.72A (1.90)

Note: Standard errors of the mean are given in parentheses. The uppercase letters are for treatment comparisons. Mean followed by the same capital letters are not significantly different at 0.05 level of significance ($P < 0.0001$). The lowercase letters are for within-treatment comparison among rows. Within-treatment values across the rows followed by the same lowercase letter are not significantly different at the 0.05 level of significance. ($P < 0.0001$).

ent PAR, respectively). Although monoculture plants had lower SLA, they exhibited 20% higher SLN than those of the barrier and nonbarrier plants resulting in greater photosynthetic rates. Plants exposed to direct irradiance, such as those cotton plants in monoculture treatment, develop thicker leaves and they generally contain higher concentration of N per unit leaf area (Campbell et al. 1990; Paul and Foyer 2001; Henderson and Jose 2005). Despite higher SLA, lower SLN in the leaves of barrier and nonbarrier plants resulted in lower photosynthetic rates (lower cluster in Fig. 5) compared with the monoculture plants. Although reductions in SLN were observed in both the barrier and nonbarrier treatments compared with the monoculture, SLN was similar for the former treatments. As a result, the variation in A among the barrier and nonbarrier treatments could not be explained based on SLN alone.

Difference in foliar N or SLN can result not only from competition for light, but also from competition for belowground resources (Mooney et al. 1981; Traw and Ackerly 1995). Since our study showed no gradient in SLN for cotton grown in barrier and nonbarrier treatments (Fig. 2), competition for N can be ruled out. A companion study by Allen (2003) showed that competition for N was not a major factor affecting productivity of the barrier and nonbarrier treatments in our system. This indicates that water was perhaps the major belowground limiting factor affecting photosynthetic rates of cotton in the nonbarrier treatment. This was supported by the A_{max} and A–C_i curves generated for the

study. Providing equal amounts of light and different levels of intercellular CO_2 resulted in varying A_{max} of cotton among treatments (Figs. 3 and 4). Lower soil water content (21.3% reduction in gravimetric soil water content) perhaps caused the lowering of A_{max} in the nonbarrier plants compared with the barrier plants. Wanvestraut et al. (2004) conducted a companion study in our pecan–cotton system and found variation in soil water potentials between the barrier and nonbarrier treatments. The average seasonal soil water potential was 55% higher (less negative) in the barrier treatment than that in the nonbarrier treatment. In another companion study on root morphological plasticity of cotton, Zamora et al. (2006a) reported that cotton in nonbarrier treatment developed lower root length density, which may also have negatively affected water uptake. Lower root length density in combination with lower soil water content may have exacerbated water stress in nonbarrier plants and thereby affected their photosynthetic capacity.

Higher WUE in nonbarrier plants also indicated drier soil conditions compared with the barrier treatment, which implies that less water was available for absorption because of competition with pecan trees. Under water stress conditions, plants tend to minimize transpiration by closing stomata to conserve and prevent excessive loss of water, which lowers stomatal conductance, thereby resulting in lower A as observed in the nonbarrier treatment (Table 3). Wanvestraut et al. (2004) also noted 36% lower water uptake by cotton in nonbarrier (0.56 $kg·plant^{-1}·d^{-1}$) compared with barrier treat-

ment $(0.88 \text{ kg·plant}^{-1}\text{·d}^{-1})$. Consistent with these findings, the nonbarrier plants in our study also showed lower E than the barrier plants. Non-exclusion of cotton roots from pecan resulted in lower E and g in nonbarrier plants than those of the barrier plants. Although the monoculture treatment had the lowest soil water content (10.4%) compared with barrier and nonbarrier treatment, E of the monoculture plants was higher in response to high air temperature and high vapor pressure deficit (data not shown) at the time of measurement. Zhenmin et al. (1998) found that higher E is needed for cotton growing in harsher environments to provide evaporative cooling effects on the leaves to prevent cell cavitation. The observation of lower E of cotton in barrier and nonbarrier plants compared with cotton plants in the monoculture treatment is consistent with that of Zhao and Oosterhuis (1998), who found a lower E rate in cotton grown under shaded conditions because of the relatively cooler environment, which indicated lower heat stress.

The nonbarrier treatment that exhibited the lowest canopy net photosynthetic index (CNPI) had the lowest biomass and lint yield. We observed significant relationships for biomass ($R^2 = 0.76$) and lint ($R^2 = 0.68$) with CNPI (Figs. 6 and 7). Optimum lint yield in our study was attained at a CNPI of approximately 65–70 μmol CO_2·m^{-2}·s^{-1} (Fig. 7). This indicated that any further increase in A would not result in an increase in yield. Cotton in the barrier treatment had a CNPI of 52.7 μmol CO_2·m^{-2}·s^{-1}, which was slightly lower than the optimum CNPI necessary for maximum yield. CNPI of cotton in the monoculture treatment was within the optimum range. This explains the yield differences between the two treatments. Our result was in agreement with other studies of cotton in Australia (e.g., Milroy and Bange 2003) and in the southern USA (Muchow and Sinclair 1994) showing increased production with increase in net photosynthesis, but only up to a certain threshold (55–60 μmol CO_2·m^{-2}·s^{-1}).

Conclusions

Results of this study showed that morphological differences in cotton leaves resulted in varying photosynthetic rates of cotton among treatments with consequences on biomass and lint yield of cotton. The barrier plants, where belowground competition for water was eliminated, not only increased their photosynthetic rates compared with nonbarrier plants, but also exhibited photosynthetic rates comparable to the monoculture. Competition for water, coupled with shading in the nonbarrier treatment, has lowered biomass and lint yield of the nonbarrier plants. Since foliar nitrogen (SLN) was similar between the barrier and nonbarrier plants, it is reasonable to assume that the performance of cotton in our alleycropping system was influenced mainly by the availability of water and light. Maximum lint yield in our study was obtained at a CNPI of approximately 65–70 μmol CO_2·m^{-2}·s^{-1}. This study demonstrates that interspecific competition between trees and crops can regulate leaf traits such as SLA and SLN of the associated crop species, which in turn influence CNPI and yield in alleycropping systems. Further, this study showed that alleycropping systems can be used to optimize production in the Southern US, provided that field management techniques such as

Fig. 6. Relationship between canopy net photosynthetic index aboveground biomass production of cotton in nonbarrier, barrier, and monoculture treatments in Jay, Florida.
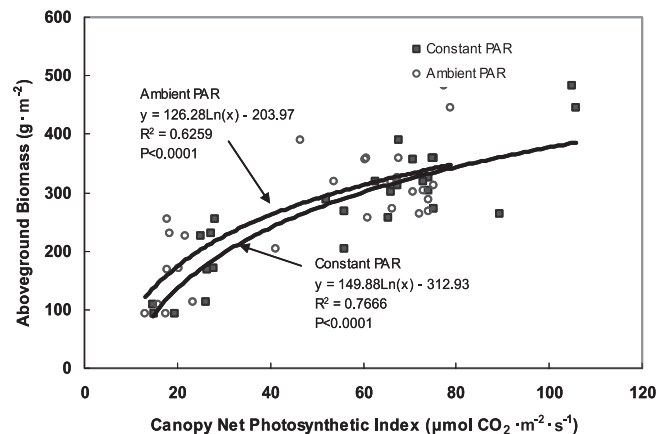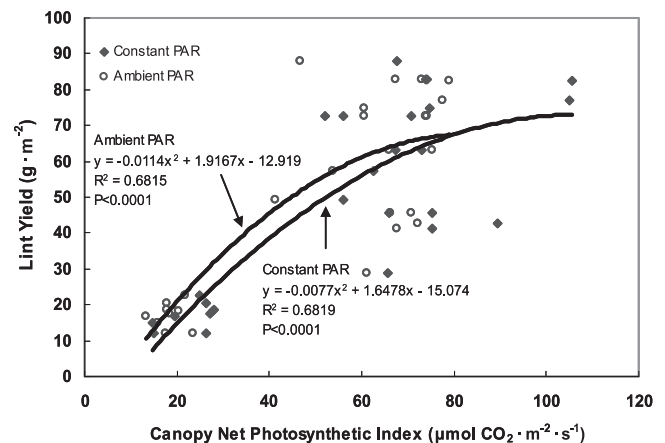

Fig. 7. Relationship between canopy net photosynthetic index and lint yield production of cotton in nonbarrier, barrier, and monoculture treatments in Jay, Florida.

trenching is employed to minimize belowground competitive interactions.

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